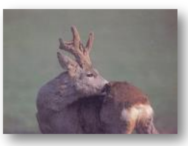
Exploited Populations

Population Modeling
University of Florida
Gainesville, FL
February-March 2016

WATERFOWL HARVEST | WATERFOWL DEMOGRAPHY | HARVEST MANAGEMENT | CONCLUSION

Waterfowl harvest: nothing new

Tomb of Khnumhotep, Dynasty 12, ca. 1897–1878 B.C, Beni Hasan, Egypt



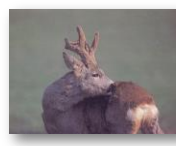
Harvest and λ
Survival

$M \rightarrow M_h = (1\text{-}h)M \qquad MV=\lambda V \Rightarrow (1\text{-}h)MV=(1\text{-}h)\ \lambda V$

Hence $M_h\ V = (1\text{-}h)\ \lambda V$

$\lambda \rightarrow \lambda_h = (1\text{-}h)\ \lambda$, asymptotic structure V unchanged

x % change in all $s_i \rightarrow$ x % change in λ



Harvest and λ
Survival

$M \rightarrow M_h = (1\text{-}h)M \qquad MV=V \Rightarrow (1\text{-}h)MV=(1\text{-}h)\ \lambda\ V$

Hence M_h V

$\lambda \rightarrow \lambda_h = (1\text{-}h)\ \lambda$, asymptoti

$s_i \rightarrow s_i\ (1\text{-}h)$
if harvest or incidental mortality
entirely before or after natural mortality.
Then $\lambda \rightarrow \lambda\ (1\text{-}h)$

x % change in all $s_i \rightarrow$ x % change in λ

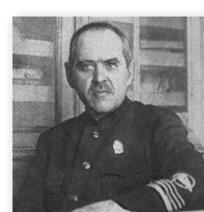
Modeling Harvest Mortality

- Not quite as simple as appears on first glance

Some History

Fedor Illyich BARANOV,
An officer of the Russian fleet,
and a pioneer of the
theory of exploited populations.

W.E. RICKER taught himself
Russian to be able to read
BARANOV's works.



Exploitation in continuous time: mortality and exploitation as competing risks *(Baranov, 1918)*

"natural" dynamics of death : $n(t+dt) - n(t) = -m\, n(t)\, dt$

with exploitation : $n(t+dt) - n(t) = -(m+h)\, n(t)\, dt$

m, h: natural mortality and harvest *instantaneous rates*

two sources of mortality assumed additive, with total rate $z = m+h$

However, the number of individuals at risk for both sources of mortality varies with total mortality z as $n(t) = n(0) \exp(-z\, t)$

Exploitation in continuous time: mortality and exploitation as competing risks over [0, T]

Number of natural deaths $\int n(t)\, m\, dt = m/z\, n(0)(1-e^{-zT})$

Number of deaths from exploitation $= h/z\, n(0)(1-e^{-zT})$

Proportion of deaths from exploitation $H = h/z\, (1-e^{-zT})$

Overall proportion of survivors $S = e^{-zT}$

Proportion of survivors if no exploitation $S_0 = e^{-mT}$

$\Rightarrow$ a complex relationship between S, H, and S_0 :

$$1 - H/(1 - S) = \log(S_0) / \log(S)$$

… S cannot be worked out as a simple function of H and S_0

Additive Risks: Instantaneous and Finite Rates

$S_0 = e^{-mT} =$ Probability that animal alive at time 0 survives nonhunting mortality sources until time *T* in the absence of any other mortality source

$1 - K = e^{-hT} =$ Probability that animal alive at time 0 survives hunting mortality sources until time *T* in the absence of any other mortality source

$S = S_0(1-K) = e^{-(m+h)T} =$ Probability that animal alive at time 0 survives all mortality sources until time *T*

Additive Risks: Instantaneous and Finite Rates

$S = S_0(1-K) = e^{-(m+h)T} =$ Probability that animal alive at time 0 survives all mortality sources until time *T*

S_0 and *K* are referred to as finite "net rates", in the sense that they are applicable when no other mortality sources are operative

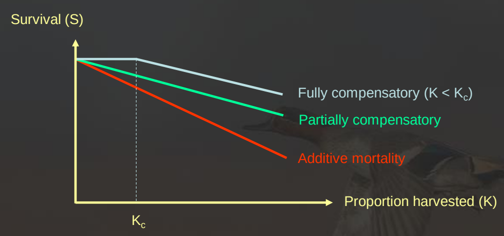
Additive Risks: Instantaneous and Finite Rates

- $S = S_0(1-K) = e^{-(m+h)T} =$ Probability that animal alive at time 0 survives all mortality sources until time *T*
- This expression holds true when the mortality sources are separated in time, e.g., hunting for (0, *T′*) and nonhunting for (*T′*, *T*)
- The above expression also holds when there is no temporal separation of the mortality sources (both sources operate throughout (0, *T*))

N. A. Waterfowl Harvest Management

- 1960s-1970s: debate over whether harvest mortality really acted as an additive competing risk
- Alternative idea was that number of birds harvested had little to do with breeding population available in spring
  - If harvest mortality increased then nonhunting mortality decreased

Model-based harvest regulation (Anderson & Burnham 1976)



Mallard hunting mortality <u>largely</u> compensatory

Investigating Effects of Harvest

- Lots of poor inference procedures used to support different views, e.g.,
- Proponents of additive mortality hypothesis would frequently plot estimated harvest and annual survival rates for different locations
- Always obtained linear negative relationship, but it resulted from a negative sampling covariance $\mathrm{cov}(\hat{h}_j, \hat{S}_j)$

Investigating Effects of Harvest

- Proponents of compensatory mortality hypothesis often confuse net and crude rates
  - Crude mortality rate is the proportion of individuals that die of focal mortality source in the presence of other sources
  - Denote crude rate with prime, e.g., S_0'
- But crude rates depend on the magnitude of other operative rates and are hence tricky to interpret

Investigating Effects of Harvest

- Year divided into hunt season followed by no-hunt season, so $S = S_0(1-K)$
- Hunting occurs first, so $K = K'$, but

$$1 - S_0' = (1-K)(1-S_0)$$

- Example:
  - $S_0 = 0.8$, $K = 0.05$, $1\text{-}S'_0 = 0.19$
  - $S_0 = 0.8$, $K = 0.15$, $1\text{-}S'_0 = 0.17$
- Inverse relationship between K and $1\text{-}S'_0$ might appear to support compensatory hypothesis, but the example shows additive mortality

Investigating Effects of Harvest: N.A. Mallards, 1987-2015

- Effects of hunting question important to management
- Boomer et al. (in review) recently undertook a thorough analysis of mallard survival and harvest rates

Harvest and Survival Estimation for N.A. Mallards

- Band reporting probabilities can vary over time and space:
  - Band inscription
  - Reporting methods
  - Recovery areas
  - Hunter behavior
- What is the relationship between harvest and survival over a time period with differing harvest regulations?

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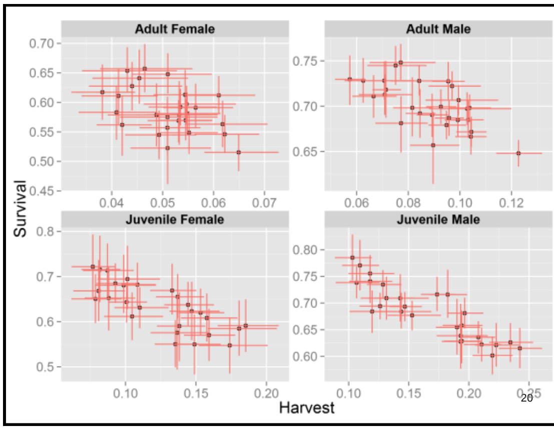
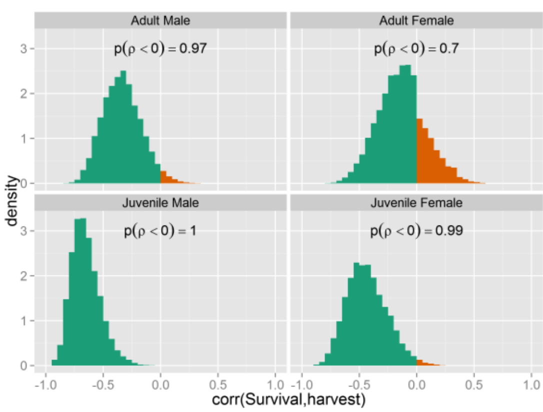
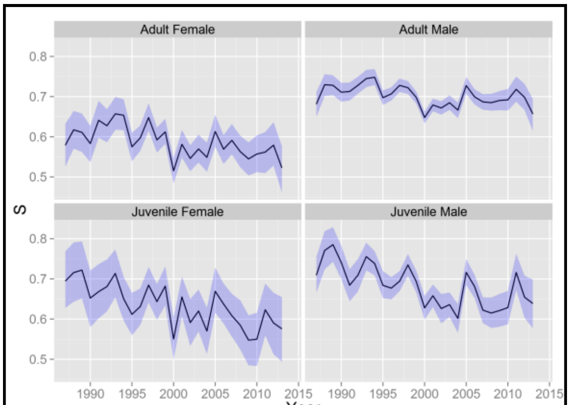
Limited Range of Harvest Rates Since 1995

- Used data from 1987 for analysis
- Included more variation in harvest rates, e.g.,
  - Adult males: 0.05 < *h* < *0.13*
  - Young males: 0.10 < *h* < *0.25*







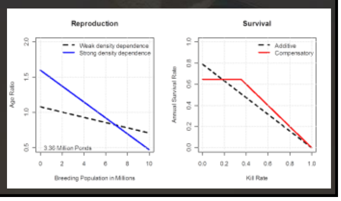
Harvest Management for N.A. Mallards

- So we now have fairly strong evidence of substantial additivity of hunting mortality
- But this analysis is new, and what about reproductive effects?
- How have we been managing mallards in the face of this uncertainty?

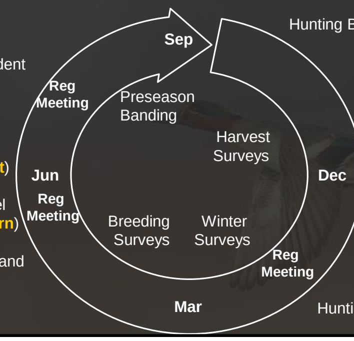
Managing harvest while facing uncertainty: Adaptive Harvest Management (AHM)

AHM of mid-Continent Mallard adopted by U.S. Fish & Wildlife Service 1995

Mid-continent mallard Model Set: ScRs, ScRw, SaRs SaRw



Managing harvest while facing uncertainty: Adaptive Harvest Management (AHM)



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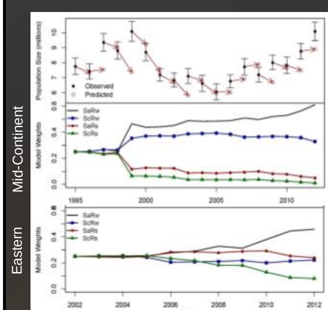
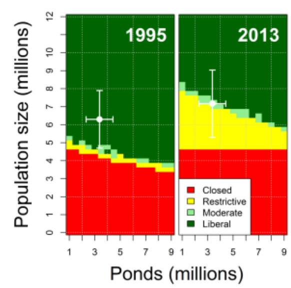
Managing harvest while facing uncertainty: Adaptive Harvest Management



Best supported model (so far):

Additive mortality
Weakly D-D reproduction

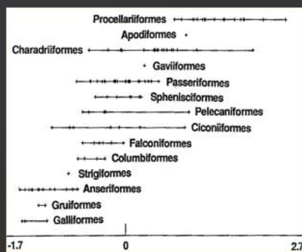
Changes in Mallard Harvest Policies with Learning



Adaptive Management Mid-Continent Mallards

- Provided a natural way to manage in the face of uncertainty
- Permitted us to learn
  - Increased “weight” on additive model is consistent with recent survival analyses
- Permitted us to use what has been learned as we proceeded

WATERFOWL: DEMOGRAPHIC CHARACTERISTICS and HARVEST



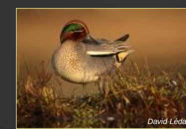
← Fast 1[st] PC Slow →

PCA of Log Age at 1[st] repro., Log Ad. life expectancy, Log Fecundity, ***corrected*** for body size
Gaillard et al. 1989, Oecologia

Also contrasted within the family:

Common Teal *Anas crecca* (Europe):

Adult annual survival = 0.485 (Devineau et al. 2010)
Clutch size = 8-12 eggs (various sources)
Sexual maturity 1 year (del Hoyo et al. 1992)



Mute Swan *Cygnus olor* (Europe):

Adult annual survival = 0.85 (McCleery et al. 2002)
Clutch size = 5-7 eggs (del Hoyo et al. 1992)
Sexual maturity 3 years (del Hoyo et al. 1992)

Harvest and adult survival among Anseriformes
Devineau Ph.D., Devineau et al., in prep.

- 53 species, with replications over populations
- Estimated annual adult survival probability (CMR, Recoveries)
- Categorical index of hunting pressure

h = 0 protected
h = 1 low hunting
h = 2 medium
h = 3 high

Espèce	Information chasse	HP
Anas acuta	"hunter effort (...) was consistently high"	2
Anas superciliosa	"exposed to heavy hunting pressure"	3
Anas platyrhynchos	"regulations were stable and relatively liberal"	2
Anas platyrhynchos	"regulations were restrictive"	1
Anser a. albifrons	"restrictive measure have been imposed on shooting"	1
Aythya collaris	"the population (...) is heavily harvested"	3
Lophodytes cucullatus	"because of their low harvest rate"	1

Harvest and adult survival among Anseriformes
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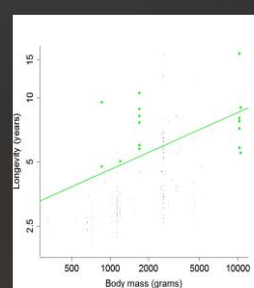

Teal Swan

F(S) = a + b Log W + c h

Protected species

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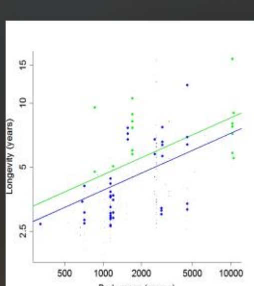

Teal Swan

F(S) = a + b Log W + c h

Low hunting pressure

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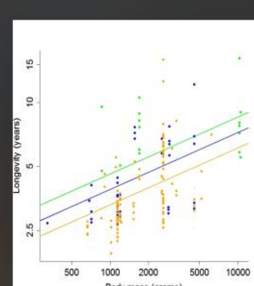

Teal Swan

F(S) = a + b Log W + c h

Medium hunting pressure

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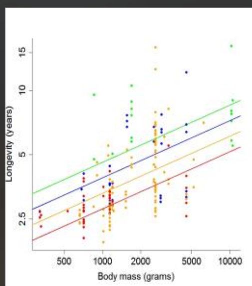

$F(S) = a + b \text{ Log } W + c \text{ h}$

High hunting pressure

Teal Swan

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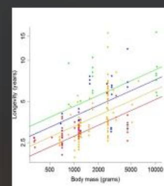

Survival does increase allometrically with body mass

Survival does decrease with hunting pressure

Hunting pressure for a given body mass quantifiable from change in survival

Protected: $S=S_0$

Low harvest: $S=S_0 \cdot (1-H_{low})$ $H_{low} \approx 11\%$

Medium harvest: $S=S_0 \cdot (1-H_{medium})$ $H_{medium} \approx 26\%$

High harvest: $S=S_0 \cdot (1-H_{high})$ $H_{high} \approx 45\%$

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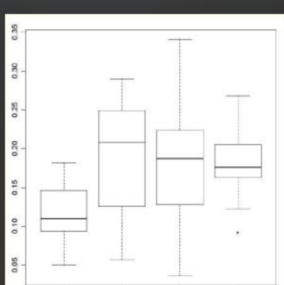
Harvest and adult survival among Anseriformes

Devineau Ph.D., Devineau et al., in prep.

Estimated harvestable proportion (λ_{max}-1)



Protected Low Medium High

Hunting pressure

Most strongly harvested species still the most able to sustain harvest

Up to ca. 20% of population: how is it sustainable?

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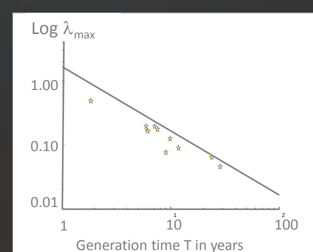
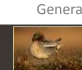
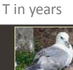
Max Pop. Growth rate per generation is invariant in birds ≈ 3

(Niel & Lebreton 2005)







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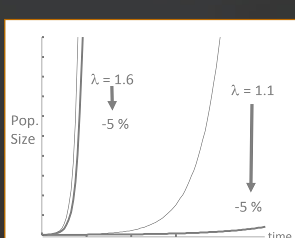


Fast waterfowl species with short generation time

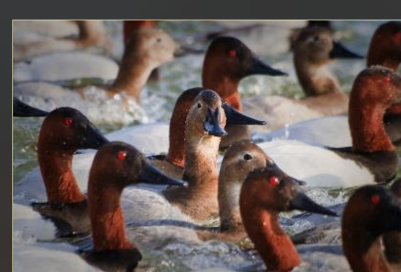
=

Greater population growth rates

=

Greater ability to sustain harvest

HARVEST MANAGEMENT IN WATERFOWL: Compensatory mechanisms?



Compensatory Mechanisms

- Original compensatory mortality hypothesis is phenomenological:

$$S = S_0(1 - bK); b \rightarrow 0 \mid K < C$$

- When it does seem to fit data, what sorts of mechanisms might be responsible?
  - Density-dependence
  - Heterogeneity

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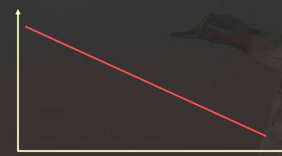
Compensation by density-dependence

Non-harvest mortality or fecundity decreases with density of individuals so that reduction in population size due to harvest leads to fitness improvement of harvest survivors.



Some evidence for DD non-hunting mortality in waterfowl (e.g. Ring-necked duck in Conroy & Eberhardt 1983)

How Might We Model Density-Dependent Survival?

- Johnson et al. (1993) proposed

$$S_t = S_{0,t}(1 - K_t)$$

$$S_{0,t} = \frac{e^{\beta_0 + \beta_1 N_t (1-K_t)}}{1 + e^{\beta_0 + \beta_1 N_t (1-K_t)}}$$

- So post-hunting season survival is modeled as a function of post-season density
  - Expectation that $\beta_1 < 0$

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Compensation by density-dependence of survival

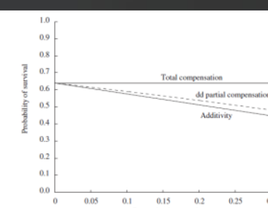

Figure 3. An example of compensation by density-dependence. Survival at density N is 0.64. Density-dependence is strong enough to make survival probability decrease to 0.48 (a 25% decrease) if population size doubles. Despite this strong density-dependence, compensation of harvest is weak, the dotted line being close to $S_0(1 - 0.825K)$.

Lebreton (2005)

➡ Compensation by DD survival is weak at best

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Compensation by density-dependence of fecundity

Survival of semi-natural Mallard nests does decrease with increasing nest density (Elmberg et al. 2009)
Similar evidence for N.A. prairies (Dzubin 1969)

Recruitment can compensate harvest if $\frac{\Delta F}{F} \approx TK$ (Lebreton 2005)

➡ Dabbling ducks with a 1.5 years generation time would need a 15% increase in F to compensate a 10% harvest: is this realistic ?

Would so many 1st year females attempt breeding without hunting ?

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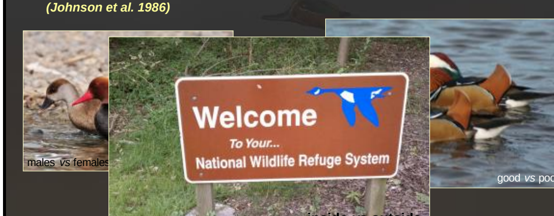
Compensation by heterogeneity

Scalar models: all individuals equivalent

Unharvested: $N_{t+1} = \lambda N_t$

Proportional harvest: $N_{t+1} = (1 - h)\lambda N_t$

This is not the real world ! Populations are heterogeneous, i.e. structured ! ***(Johnson et al. 1986)***



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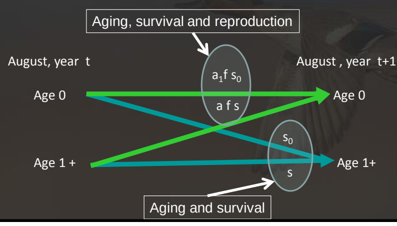
Compensation by heterogeneity: a duck population model

- Life cycle, hypothetical duck population
- Post-breeding pulse representation

s_0 : 1st year survival probability
s : after 1st year survival probability
f : number of females fledged / female
a_1 : 1st year breeding probability
a : after 1st year breeding probability



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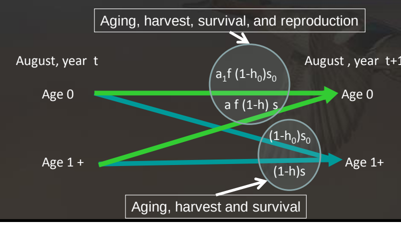
Compensation by heterogeneity: a duck population model

- Life cycle, hypothetical duck population
- Age-specific harvest probabilities h_0 and h
- Easily translates into a matrix pop. model
- Simulation + Theoretical results



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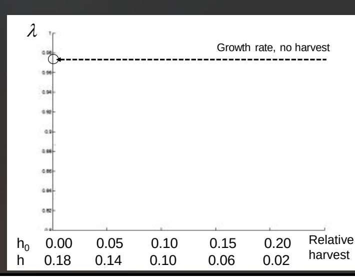
Compensation by heterogeneity: simulation



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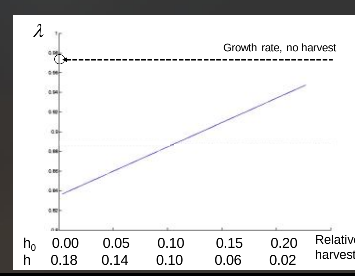
Compensation by heterogeneity: simulation

- By varying h_0 and h in opposite directions, keep overall harvest = 0.10 (10 %)



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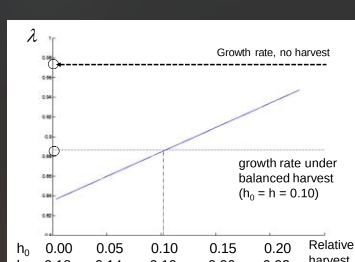

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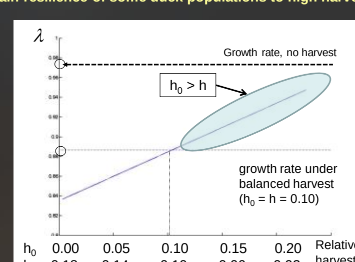
Compensation by heterogeneity: simulation

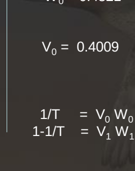
- By varying h_0 and h in opposite directions, keep overall harvest = 0.10 (10 %)
- When h_0 > h, attenuated impact on population growth rate
- Simulates the well known imbalance of (relative) harvest towards young ducks
- Could explain resilience of some duck populations to high harvest rates



Compensation by heterogeneity: Theoretical results

- Changes in h_0 and h are changes in overall survival $s_0(1-h_0)$ and $s(1-h)$
- Effect on growth rate λ depends on elasticities (« relative sensitivites »)
- Sensitivities can be expressed as a function of generation time T = 5.5167 y

Age class	0	1+
Stable asymptotic structure	$W_0 = 0.4521$	$W_1 = 0.5479$
Reproductive value (=contribution to growth)	$V_0 = 0.4009$	$V_1 = 1.4943$
Elasticity		
$\partial \log \lambda / \partial \log s_0$	1/T $= V_0 W_0 = 0.1813$	
$\partial \log \lambda / \partial \log s_1$	1-1/T $= V_1 W_1 = 0.8187$	



Compensation by Heterogeneity

- Estimation and modeling are much easier when heterogeneity is associated with an identifiable characteristic such as age
- What about individual frailty?
  - Vital rate variation among individuals not associated with any identifiable characteristic (can't tell quality of bird in hand)

Compensation by heterogeneity: Individual Frailty

Lindberg, Lebreton, Boomer, unpublished

- Canvasback *Aythya valisineria*
- 2 classes of "demographic quality" (purely phenotypical)
  POOR and GOOD
- A discrete mixture model for a continuous heterogeneity
- "POOR" individuals more vulnerable to hunting than "GOOD"

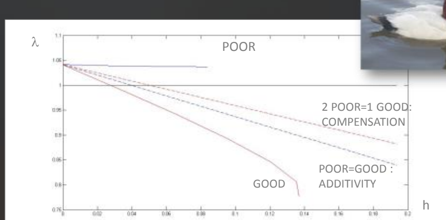
Compensation by heterogeneity: Individual Frailty

Lindberg, Lebreton, Boomer, unpublished

	AGE	1	1	2+	2+
	QUALITY	POOR	GOOD	POOR	GOOD
AGE	QUAL ITY				
1	POOR	0	$a_{1g}*f_{gp}*S_{1p}*(1-h_p)$	$a_p*f_{pp}*S_{1p}*(1-h_p)$	$a_g*f_{gp}*S_{1p}*(1-h_p)$
1	GOOD	0	$a_{1g}*f_{gg}*S_{1g}*(1-h_g)$	$a_p*f_{pg}*S_{1g}*(1-h_g)$	$a_g*f_{gg}*S_{1g}*(1-h_g)$
2+	POOR	$S_p*(1-h_p)$	0	$S_p*(1-h_p)$	0
2+	GOOD	0	$S_g*(1-h_g)$	0	$S_g*(1-h_g)$

Compensation by heterogeneity: Individual Frailty

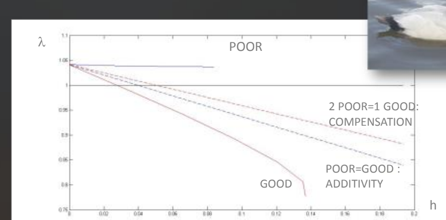
Lindberg, Lebreton, Boomer, unpublished

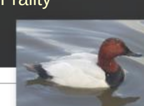


"POOR" individuals more vulnerable to hunting than "GOOD"
"Die from hunting before dying from other cause"
Even under exchange between POOR and GOOD

Compensation by heterogeneity: Individual Frailty

Lindberg, Lebreton, Boomer, unpublished





Intimately linked with REPRODUCTIVE VALUE
P1 = 0.1544 G1 = 1.1233 P2+ = 0.2233 G2+ = 1.1233
Contribution to future growth is the common currency for harvest

Reproductive Value (RV) and harvest (MacArthur 1960)

Compensation by heterogeneity

=

harvest of low Reproductive Value

Biologically significant iff RV strongly uneven

RV(autumn) < RV(spring)
RV(young) < RV(adult)
RV(sink) < RV(source)
RV(ill) < RV(healthy)
...

Harvest and Heterogeneity

- Heterogeneity/variation that is readily observed (age, sex, location, etc.) can be:
  - Easily dealt with in inference and modeling
  - Exploited to maximize harvest (focus harvest on individuals of low reproductive value)
- Heterogeneity in vital rates that is not readily observed can:
  - Make inference more difficult (requires mixture distributions)
  - Lead to misinterpretations (see exercise)

Managing Exploited Populations I

- Management focus is on how exploitation influences vital rates (rates of birth, death, movement)
- Historically: focus on manner in which hunting mortality interacts with nonhunting mortality to produce overall mortality
- Additive, independent competing risks provide a theoretical framework for this (Baranov 1918), just as they do for most disease modeling

Managing Exploited Populations II

- Anderson-Burnham (1976) brought discussions of hunting effects into the scientific arena by defining additive and compensatory mortality hypotheses
- Mechanisms that could underlie compensation are density-dependence and heterogeneity
- But additive competing risks underlie both mechanisms

Managing Exploited Populations III

- Density-dependence:
  - Additive mortality risks, with nonhunting risks modified by post-hunting season density
- Heterogeneity:
  - Additive mortality risks, with “compensation” effected by positively correlated vital rates (good and poor with respect to both hunting and nonhunting mortality) and resultant changing group composition

Managing Exploited Populations IV

- Although density-dependence and heterogeneity have been discussed primarily as mechanisms underlying mortality responses, they apply to reproduction and movement as well
- Given fair knowledge of population responses to harvest, management can be based on models such as those discussed in this class

Managing Exploited Populations V

- But what do we do in the more typical case of process uncertainty (i.e., about how the population responds to harvest)?
- Adaptive management can use multiple process models and is a defensible approach leading to:
  - State-dependent management based on current state of knowledge (estimated system and information state)
  - Learning (changes in information state)